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BIRDS COLLECTED DURING THE WHITNEY SOUTH SEA EXPEDITION. XXVII¹

NOTES ON THE VARIATION OF IMMATURE AND ADULT PLUMAGES IN BIRDS AND A PHYSIOLOGICAL EXPLANATION OF ABNORMAL PLUMAGES

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A study of the immature plumages of *Neolalage banksiana* (Gray) has brought out some interesting facts concerning the physiology of feathers and has led to an investigation of some problems concerning the variation of plumages of birds with age. The results of a study of skins have been compared with the recent advances in the field of experimental physiology, and an attempt has been made to explain the physiological causes of certain abnormal plumages, which thus far have been very puzzling to the ornithologist. I am indebted to Dr. G. Kingsley Noble for a helpful discussion of the problems of the physiology of the bird feather.

HISTORICAL REVIEW AND SUMMARY OF OUR PRESENT KNOWLEDGE ON ABNORMAL IMMATURE AND ADULT PLUMAGES OF BIRDS

In the preceding paper,² I described the normal immature plumage of *Neolalage banksiana* (Gray). This plumage vaguely resembles the adult plumage, but the parts of the plumage that are blackish in adult birds are grayish or brownish, all other colors are less intense, and the whitish patterns less pure. This seems to be the more primitive type of immature plumage. However, quite a number of specimens wear a different immature plumage which approaches in its coloration the adult plumage.

This seems to be another case of what is termed in the recent ornithological literature as "retarded" and "progressive" plumages. The presence of two immature plumages suggests of course immediately two further possibilities: one is that there is a fourth plumage (a prenuptial plumage) inserted between the immature and the adult plumage, and the other that the birds described as having a "progressive" first-year plumage are molting the body plumage from the first-year (=immature)

¹Previous papers in this series comprise American Museum Novitates, Nos. 115, 124, 149, 322, 337, 350, 356, 364, 365, 370, 419, 469, 486, 488, 489, 502, 504, 516, 520, 522, 531, 590, 609, 628, 651, and 665.

²American Museum Novitates, No. 665, pp. 1-5.

plumage to the adult plumage. A careful study of more than twenty-five birds in the first-year plumage (including several molting specimens) convinced me that neither of these two alternative possibilities can be accepted. Furthermore, the case that a bird has two types of first-year plumage (a progressive and a retarded one) is not unusual.

So far as I know these plumages for the first time were correctly identified in the Black Redstart (*Phoenicurus ochrurus gibraltariensis* (Gmelin)) of Europe. Kleinschmidt (Berajah, *Erithacus Domesticus*, pp. 9–12, 1907–1908) gave a fairly clear picture of the various plumages although he did not realize all the complications. In this species two juvenal plumages are now known: one grayish one, similar to the female plumage (*cairei*-plumage, Gerbe), and one blackish one, similar to the fully adult male (*paradoxus*-plumage, C. L. Brehm). It was also known that even in the adult plumage of the male a grayish phase is possible, a fact not appreciated by Kleinschmidt. This author however pointed out that there is a possible geographical variation in the proportional frequency of the two juvenal plumages. He found relatively many more “*paradoxus*” juveniles in his material from Spain and Asia than among his central European birds, but left open the question as to whether or not this was merely accidental.

Stresemann, in his monograph of the Macedonian bird fauna¹ added considerably to the elucidation of the problem. He coined the term “Fortschrittskleid,” for what I call in this paper “progressive plumage,” and “Hemmungskleid,” for what I call “retarded plumage.” He also called attention to the fact that this divergence of first-year plumages is not peculiar to the species *Phoenicurus ochrurus*, but recorded it for four other species (*Muscicapa hypoleuca*, *op. cit.*, p. 119; *Muscicapa albicollis*, *op. cit.*, p. 121; *Sylvia atricapilla*, *op. cit.*, p. 138; and *Sylvia communis*, *op. cit.*, p. 141). Further facts brought out in this stimulating work are that such plumages may also occur in adult birds: namely, “retarded” plumages in adult males (*op. cit.*, p. 176) and “progressive” plumages in adult females (*op. cit.*, p. 174).

Obviously such plumages occur in many species of birds (as for example in the American redstart and the orchard oriole), but it is not my task here to collect all such cases, particularly since the significance of those plumages was usually not recognized by the authors describing them. It would make it necessary to examine their material again. I will therefore cite only a few more instances in which these plumages were definitely termed “progressive” and “retarded.”

¹1920, ‘*Avifauna Macedonica*,’ München, p. xvi.

There is a detailed paper on the snow bunting (*Plectrophenax nivalis*), by Natorp,¹ in which the author emphasized the fact—already mentioned by Stresemann—that the divergence of plumages is not restricted to the first-year dress but can also occur in the adult male, and even in the female plumage. He found some atypical females that showed a distinct approach toward the male plumage, without being actually cockfeathered.

These two plumages, however, are not always sharply defined; many specimens are somewhat intermediate, a fact first brought out by Kleinschmidt in his paper on the black redstart, and also mentioned by Natorp.

In the course of my revisions of Polynesian genera I have come across several cases of such dimorphic plumages. It may be worth while to recapitulate my previous findings.

I first noticed the two phases of juvenal plumage in the genus *Erythrura* (Amer. Mus. Novit., No. 489, p. 8), but insufficient material prevented me from discussing the details. However, it is clear that at least in the species *Erythrura cyanovirens* there are two immature plumages, one being typical and the other showing an approach toward the adult male.

A doubtful case is presented by *Ptilinopus solomonensis ambiguus* Mayr (Amer. Mus. Novit., No. 504, p. 7). We have here several specimens resembling very much the adult birds, but approaching in certain minor characters the juvenal plumage. These birds may wear a "first-year plumage," but since such a plumage is unknown from any other pigeon, they may also be adult birds in a "retarded" plumage. A tendency toward a "progressive" juvenal plumage occurs in the genus *Myzomela*, but the phenomenon does not seem to be universal in this genus (Amer. Mus. Novit., No. 516, p. 18).

The genus *Pachycephala* is the first one encountered by me, where "progressive" and "retarded" plumages are quite common. But since the usual juvenal characters are not well defined in all the subspecies, it is sometimes difficult to decide whether a certain specimen is a juvenal bird in a "progressive" plumage, or an adult bird in a "retarded" plumage. Size of testes and shape of wing and tail indicate that most of these birds are in a "retarded" adult plumage (Amer. Mus. Novit., No. 522, pp. 2, 11, 13, 14, 16–21; No. 531, pp. 4, 13, 15, 21). It is interesting to note that such unusual plumages are quite frequent in some of the subspecies, but entirely lacking in others in spite of the considerable material available.

¹1931, Journ. f. Ornith., pp. 338–346.

Adult males in a "retarded" plumage and adult females with a "progressive" plumage are also found in the species *Clytorhynchus nigrogularis* Layard (Amer. Mus. Novit., No. 628, p. 17) and in the genus *Myiagra* (Amer. Mus. Novit., No. 651, p. 6).

Familiarity with all these cases of abnormal plumages makes it easier to understand the plumages of *Neolalage* in which genus, however, conditions are not so clear as in most of the cases just mentioned. There are many complicating features and the material at hand is not sufficient to clear up all of the doubtful points. The best way of presenting my findings seems to be to discuss in detail the plumages of the not typically adult specimens and summarize afterwards the probable interpretation of the data.

DETAILED DESCRIPTION OF IMMATURE SPECIMENS OF *Neolalage banksiana* (GRAY)

EFATE ISLAND

Nos. 212865 and 212866.—Immature females, ovaries "small," June 1926.

Both birds are in the typical female immature or first-year dress. No remains of the downy nestling plumage can be found, nor any approach toward the adult plumage (description Amer. Mus. Novit., No. 665, p. 2).

No. 212862.—An immature female with "small" gonads, June 1926.

The bird has an essentially typical first-year plumage. The crown however is slightly darker than in the two birds just described, the collar on the throat is slightly darker, with a few feathers adorned with blackish tips, the scapulars with a few blackish feathers and practically all the upper tail-coverts with black bases. These blackish feathers belong unquestionably to the same generation of feathers as the other immature feathers and cause me to classify the specimen as an intermediate progressive plumage.

Nos. 212860 and 212861.—Two immature males with "small" testes, July 1926.

Both birds represent the typical first-year plumage of the male of this species. This plumage is very similar to the equivalent female plumage, but it differs in a few minor points. The relative wideness of the breast-band and its much more blackish coloration are conspicuous.

No. 212857.—Immature male, size of testes "minute," June 1926.

This bird wears a puzzling plumage. The bill is yellow brown and the wing (with the exception of the lesser upper wing-coverts) as in typical immature birds. However, the underside resembles very much that of the adult bird, although the white feathers of the throat are not quite so long and the black breast-band not so deeply black; the tail-feathers are brownish and immature looking at the tip, but get more and more blackish toward the base; the upperside (crown, back, scapulars, rump, and upper tail-coverts) are a mixture of immature and adult-like feathers. Most of

the latter lack the deep glossy-black appearance of a back feather of the adult bird. They are dull black frequently with a brownish-black tip. In between these feathers are some that are more brownish, and some that are grayish brown, similar to the feathers of a typical immature male; the lesser upper wing-coverts are blackish, and the median wing-coverts with broad pure white tips. Some of the characters of this bird strongly suggest a molting condition, particularly the diversified character of the plumage. Against this there are several arguments: first, June (when the specimen was collected) is not the molting season; secondly, I could find no feathers in sheets; and thirdly, even those feathers that approach the adult plumage are not so deeply or brightly colored as typical adult feathers.

EPI ISLAND

No. 216082.—Immature female, ovaries "small," December 1926.

This bird is very similar to No. 212857 from Efate, but in accordance with the season much more worn. One of the tail-feathers is being replaced by an adult one. Otherwise there are no signs of molting. The bill is blackish, not yellowish brown.

PENTECOST ISLAND

No. 216084.—Molting male, testes "swelling?," January 1927.

This bird molts from a progressive first-year plumage (as revealed by the color of the tail-feathers) into a normal adult male plumage.

AURORA ISLAND

No. 217940.—Molting male, testes "large," January 1927.

This bird again is very puzzling. It seems to have just begun to molt from a "progressive" first-year plumage into the next plumage. But most of the new feathers, appearing in the wing and hind neck, are dull blackish, not vividly black as fresh adult feathers usually are.

No. 217942.—Molting female, ovaries "small," January 1927.

This bird is molting from a progressive immature plumage into an apparently normal adult plumage. A good part of the body plumage of the upperside has been changed already, as have some of the tail- and wing-feathers. Most of the feathers of the underside, however, seem to belong to the first-year plumage. The breast-band is broad and dull black. The bill is blackish.

VANUA LAVA ISLAND

No. 216073.—Immature female, ovaries "small," November 1926.

This bird is very similar to No. 212857 from Efate, except that crown, back, and breast-band are duller black and the upper throat not as pure white. The bill is dusky brown.

AOBA ISLAND

No. 217947.—"Young" male (= testes small), January 1927.

This bird is in the typical immature plumage, similar to Nos. 212860 and 212861 from Efate. The specimen is apparently in fairly fresh plumage and shows neither any signs of molting nor any approach toward the adult plumage. The bill is blackish, instead of yellowish as in most immature birds.

No. 217944.—Molting male, testes "small," January 1927.

This bird is in the middle of the molt from a typical immature plumage to the normal adult plumage. The replacement has already taken place on head, throat, upper back, and part of the rump; new feathers are molting in on all other parts of the body; wing and tail are in the middle of the molt.

SANTO ISLAND

No. 214189.—Immature (II) male, testes "small," September 1926.

This bird wears a typical "progressive" plumage. The black on the upperside is somewhat dull and some of the feathers have brownish edges. Wing- and tail-feathers are typical for these progressive plumages. They are immature near the tip and assume more and more adult characters toward the base. Bill black.

No. 214190 and 214191.—Immature (II) male, testes "small," August 1926.

Both birds very similar to No. 214189, but the bill more or less yellowish.

No. 216077.—Immature (II) male, testes "large," December 1926.

This bird is in the same plumage as the three birds just described although the testes are indicated as large. The bill is yellow and the skull not yet ossified.

No. 216079.—Immature (II) male, testes "small," December 1926.

This specimen is particularly interesting since it proves conclusively that the progressive immature plumage follows immediately the nestling plumage. There are still quite a number of the downy nestling feathers, particularly on the sides of the throat, in the middle of the abdomen and on the upper tail-coverts. The immature plumage is of a very progressive type with the tail, for example, almost indistinguishable from an adult tail.

No. 214196.—Immature (II) female, ovary "small," September 1926.

A typical immature bird in progressive plumage. Several feathers on the back either brownish or with brown edges. Bill black.

No. 214198.—Immature (II) female, ovary "small," August 1926.

Similar to preceding, but bill yellow at base. Skull not ossified. This bird has a body-plumage colored as richly as an adult bird. Wings and tail are also of a very progressive type. In this, as in all those birds with a progressive plumage, the lesser upper wing-coverts as well as some other upper wing-coverts are very similar to the equivalent adult feathers. I could find no evidence that these feathers were not acquired immediately after the nestling plumage, but certain specimens point to the possibility of a prenuptial partial molt in this part of the body. It is still a doubtful point and needs further investigation based on better material.

Nos. 214197 and 214199.—Immature (II) females, ovaries "small," August 1926.

Both birds wear a progressive plumage, but not so pronounced as the two preceding specimens, all the black tones being distinctly duller and with a brownish admixture. Bills brownish.

No. 214195.—Sex indetermined [? ♀], immature, September 1926.

This specimen is particularly interesting since it molts from the nestling to a progressive immature first-year plumage. Soft, downy nestling feathers are retained in the middle of the abdomen, on the under tail-coverts, on the upper tail-coverts, and a few feathers on the scapulars and on the upper back; the rest of the plumage is made up of feathers of the first-year plumage of a rather pronounced progressive type. This specimen also shows that the lesser upper wing-coverts do not belong to the nestling plumage but are molting in with the rest of the first-year body-plumage, while the greater upper wing-coverts and the primary coverts are acquired together with the wing in the nestling plumage. The bill is black with a yellow base.

MALEKULA ISLAND

Nos. 213730, 213731, 213740.—Three immature males, testes "small," August 1926.

All three birds wear a "progressive" first-year plumage. Head and back rather blackish, with relatively few feathers with brownish edges. Bills yellowish brown.

No. 213738.—Immature male, testes "small," August 1926.

This bird really resembles the female in a progressive first-year plumage much more than it resembles the male. However, the large measurements prove the correctness of the sex indication on the label. The bird has crown and back dark grayish with paler or brownish edges; bill yellowish brown.

Nos. 213744, 213745, 214200.—Three immature females, ovaries "small," August 1926.

These three birds are in an intermediate plumage, not quite so blackish and "progressive" as most immature males; most feathers of crown and back with grayish or brownish edges; wings immature, tail immature on tips, blacker toward the base; no signs of molting; bills yellowish brown.

SUMMARY

Summarizing the results of the investigation of these plumages I can state the following facts:

1.—The first-year plumage of *Neolalage banksiana* (Gray) shows two types of plumage: one, apparently more primitive, with a less intense pigmentation, which may be called a "retarded" plumage; and the other, approaching in pigmentation the adult dress, which may be called a "progressive" plumage.

2.—There is no clear-cut division between these two plumages; several specimens are intermediate in their characters.

3.—There is a definite geographical correlation between the frequency of the two plumages on the various islands. On certain islands (as Efate and Aoba) all, or the majority, of the first-year birds wear a "retarded" plumage; on other islands (as Santo and Malekula) all, or the majority, of the first-year birds wear a "progressive" plumage.

4.—The sexual dimorphism is frequently more pronounced in the first-year plumage than in the adult dress. Adult males and females are very much alike in this species, but the first-year plumage of the male is usually much more “progressive” than that of the female.

5.—The “progressiveness” of an individual feather depends a great deal upon the time of its molt. Those feathers of the first-year plumage that grow first, as the wing-feathers and certain of the wing-coverts, resemble the adult feathers least. In some cases, feathers with a much more immature appearance (having grown earlier) can be found adjoining feathers with decidedly more adult characters.

6.—The changing of the physiological status toward the adult condition can be observed in many individual feathers (particularly the tail-feathers). The tip of such a feather greatly resembles an equivalent typical immature feather, while the base is more like that of an adult feather.

7.—Progressive feathers of the first-year plumage resemble adult feathers not only in pigmentation but frequently also in structure. This makes it quite difficult in extreme cases to decide whether a certain specimen is a first-year bird in “progressive” plumage or an adult bird in “retarded” plumage.

PHYSIOLOGY OF IMMATURE AND ADULT FEATHERS

When I first encountered these abnormal plumages I thought that they reflected the development of the gonads during the time of the molt. The same opinion is expressed by Alden H. Miller in his study on progressive first-year plumages in *Phainopepla nitens*.¹ He says (p. 435): “The second variable, that of pigmentation, must be associated with the gonads and probably is the result of a varying degree of development of the hormone-secreting tissues of the testis at the time of molt.”

However, there are two serious objections to this. The first one is that the condition of the gonads as indicated by the collectors on the labels of these birds do not agree with Miller’s suggestion. Quite frequently we find specimens that, according to their plumage condition, must have left the nest but a few days or weeks and were molting from the downy nestling plumage to a progressive first-year plumage. These birds have minutely small testes and would not have shown any development of their gonads for the next six or eight months.

On the other hand there are the birds that breed in a retarded plumage and molt into this retarded plumage with the gonads decidedly more

¹1933, University of California Publ. in Zool., XXXVIII, No. 13, pp. 425–446.

developed than those birds that molt from the nestling plumage into a progressive first-year plumage.

The other reason for my conviction that the type of plumage that is acquired through the postnatal and prenuptial molt is largely independent of the gonad hormones is based on a study of the experimental data. This I shall illustrate by the following few examples, without attempting to review the entire extensive subject.

There are many complications in the various genera and orders of birds, but the case of the domestic fowl enables us to explain most of the phenomena of plumages. Taking a normal race of fowl we have the following sequence of plumage.

- I.—Downy chick
- II.—Juvenal plumage, male and female similar
- III.—Adult plumage, strong sexual dimorphism

Adult roosters as well as adult hens acquire at the next molt after castration a "Neutral Plumage," which is practically the same for both sexes and greatly resembles the plumage of the adult male. It may be emphasized that the removal of the gonads does not cause the acquisition of an immature type of plumage at the next molt. Equally, if a newly hatched chick of either sex is castrated, its plumage does not retain an immature appearance all through life, but at subsequent molts it acquires first a more or less normal juvenal plumage¹ and then a "Neutral Plumage." This "Neutral Plumage" is alike in both sexes in practically all the cases that have been investigated, but in the house sparrow (*Passer domesticus* Linnaeus) the "Neutral Plumage" is dimorphic and sex-limited.² This simple scheme is slightly complicated in those cases in which there are two molts during the year and accordingly two different adult plumages, one nuptial and one internuptial plumage.

In the case of the European black-headed gull (*Larus ridibundus* Linnaeus) it has been proved by van Oordt and Junge³ that the nuptial plumage (alike in male and female) is no longer acquired after castration and that the "Neutral Plumage" is apparently identical with the internuptial or winter plumage.

The independence of the plumages from the testis hormone is still more pronounced in *Anas platyrhynchos*. Castration of the drake does not prevent a molt into the hen-feathered eclipse plumage.⁴ As may be ascertained by experimental plucking of feathers the plumage cycle is

¹Zawadowski, M., 1926, *Biologia Generalis*, II, pp. 631-638, Pl., xxxi-xl.

²Keck, Warren N., 1932, 'Control of the Sex Characters in the English Sparrow, *Passer domesticus* (Linnaeus),' *Anat. Rec.*, LIV, Suppl., p. 77.

³Van Oordt, G. J., and Junge, G. C. A., 1933, *Roux's Archiv*, CXXVIII, pp. 166-180.

⁴Kuhn, O., *Roux's Archiv*, CXXVII, pp. 519-535.

definitely fixed. There is a latent tendency from the middle of July to April to develop nuptial feathers and from May to the middle of July to develop eclipse feathers. In other words, the bird can acquire nuptial feathers only during a fixed part of the year during which the testes may be in a resting, in a developing, or in a fully developed condition, and similarly the bird can grow eclipse plumage feathers only during a fixed part of the year, no matter whether the gonads are active during this period or absent (as in the castration experiment).

All these observations and experiments allow the following interpretation: one of the phenomena of reaching maturity in birds is a gradual change in the structure and pigmentation of the feathers from an immature plumage to a neutral adult dress. This change appears to occur in steps as expressed in the successive molts required to produce the final plumage, but is actually caused by a slow physiological change, as has been proved by plucking feathers between molts.¹ This process is modified by an additional differentiation caused by a female or male hormone, which changes the neutral plumage to a typical female or male adult plumage. This latter process can be reversed by the removal of the gonads, while the change from the immature plumage to the "Neutral Plumage" seems to be irreversible and independent of any hormones thus far known.

It seems apparent that the time in which the organism changes from an immature to an adult condition (as expressed by the feathers growing at that time) is not entirely fixed. In most species it seems to occur at approximately the same age in all individuals, and in those species we do not find the abnormal plumages described above. In other species there is less uniformity. Certain individuals reach the adult condition earlier and acquire along with the first molt a plumage approaching the adult dress ("progressive" plumage), other individuals acquire a normal immature plumage with the first molt and with the second molt a normal adult plumage, and still other individuals do not reach the adult condition before the second year and thus acquire first a "retarded" adult plumage. Of course this sequence will be somewhat modified by the time and the number of molts in the various species and genera.

¹Kuhn, *op. cit.*, pp. 503-519.